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ADVANCES IN OUR KNOWLEDGE OF THE HONEY-GUIDES

By Herbert Friedmann

In the following pages I have brought together new information on various aspects of the biology of the honey-guides that has come to attention since the publication of my book in 1955. Together with these additional data, I have made such comments as seem necessary, either for their proper evaluation or for their allocation with respect to earlier knowledge. Only two phases of honey-guide studies are not included: Purely systematic data, and my continuing investigations on wax digestion, the results of which will be presented separately.

In addition to such notes as have appeared in print and which are here collated, I am indebted to the following for unpublished observations: J. P. Chapin, W. R. Ingram, C. H. Jerome, D. W. Lamm, H. M. Miles, B. Neuby-Varty, R. H. Stevenson, V. G. L. van Someren, and J. M. Winterbottom.

Additional Data on Eggs and Egg-Laying

Because of the difficulties attached to study of ovulation in parasitic birds, one must always be alert for incidental data bearing on this topic. The new information is as follows:

1. Greater honey-guide, *Indicator indicator*

One observation bearing on the time of day of ovulation comes to me from J. M. Winterbottom. On Sept. 16, 1943, in the northwestern corner of the Livingstone District, Northern Rhodesia, he caught a female greater honey-guide on the nest of a hoopoe in a hole in an ant hill. The bird had already laid its egg. He watched it go to the nest, and walked up at once, so it was only a matter of seconds, half a minute at the most, that the bird was on the nest. In answer to my query, Winterbottom informs me that this took place during the hot part of the day, between 11 a. m. and 2 p. m.

A female collected April 28 at Enugu, eastern Nigeria, by Serle (1957, p. 415) had two large yolked ova in the ovary and two ruptured egg follicles, indicating that at least four eggs would have been laid. It may be recalled that earlier data of the same type (Friedmann, 1955, p. 136) suggested, in one case at least, that eight eggs would have been laid by one bird. We still do not know what the usual number may be.

Recently, H. A. Roberts (1956, p. 114) has stated that, when about to lay in a barbet's nest, the hen honey-guide goes there accompanied by the male, and that the latter acts as a lure to draw away the potential hosts from their nest, thereby giving the hen the chance to enter it and deposit an egg. Roberts writes that the female barbet rushes out of the nest hole as the honey-guides approach, and back into it again as they depart a short distance, this performance "being repeated until she becomes rather exhausted. At this stage the female honey-guide conceals herself nearby, and as soon as both barbets pursue the increasingly bold male honey-guide, the female honey-guide makes a dash for the hole. Usually a short lull among the contestants now follows which enables the female honey-guide to deposit her egg. Should the barbets try and return too soon, the male honey-guide at once takes action to lure them away . . . ." This account is comparable to one by Millar which I have previously described (Friedmann 1955, pp. 136–137), and as I wrote then, it is "difficult to believe that the male accompanies the female to the nests of the potential hosts, as there are no data suggesting anything comparable to mating in these parasites. That the male should act as a foil, to draw off the barbets on guard while the female deposits her egg, seems like too good a story not to have entered into the recording of whatever may have actually transpired." In the case described above by Winterbottom, no male honey-guide was noted. However, we still have so few direct observations of the act of egg deposition that it is advisable to keep an open mind on this matter, even though it seems rather unlikely that the males attend the laying females.

2. Sharp-billed honey-guide, *Prodotiscus regulus*

Serle (1957, pp. 416–417) collected a female at Enugu, eastern Nigeria, on September 27 that had an egg in membrane in the oviduct and three large yolked ova and two ruptured follicles in the ovary, indicating that at least five eggs could have been laid.

Additional Host Records

Our knowledge of the life histories of all the honey-guides is still so imperfect that it is to be expected that additions to the lists of known victims will be made for a long time to come. Besides these new host species, further data on previously poorly documented ones have also come to attention in the past three years. The total supplementary data, presented here under the various species of honey-guides, do not change the present picture materially but merely add to the total recorded information and help to orient more properly some of the earlier information.

1. Scaly-throated honey-guide, *Indicator variegatus*

One additional host has been recorded for this still infrequently observed honey-guide. The case is of sufficient interest to quote the original account in some detail.

Jackson's tinker-bird, *Pogoniulus bilineatus jacksoni* (Sharp)

Van Someren (1956, p. 220) writes that

> . . . at another nest I knew to hold young, I noted fresh chippings on the ground and thought perhaps another hole was being started, but there was no such cavity. Sitting down in cover, I heard dull tapping coming from the nest hole, then noticed chippings coming out . . . . With a sharp knife, I cut a circular opening . . . and exposed the nest. The chamber and tunnel had been considerably enlarged and within was a three-quarters grown variegated honey-guide. It was remarkable that the hen honey-guide had been able to force her way in and lay her egg in the original small chamber, and moreover, how did the barbets come to appreciate that the chamber was too small to accommodate the chick! Yet, here they were, enlarging the chamber to ensure the comfort of their foster child! I replaced the circle of wood and sealed it in. The young honey-guide was seen in the forest two weeks later, attended by the foster parents . . .

It is fortunate that, in this case, the young parasite was feathered sufficiently to make its identification certain. In my book (1955, p. 105) I listed one record for the Uganda race of this tinker-bird, *Pogoniulus bilineatus nyansae* (Neumann), and echoed Jackson's (1938, p. 734) doubts that either *Indicator variegatus* or *I. indicator* could possibly get inside the small nest opening to lay there, or that the young parasite, when ready to leave, could get out through it. It now appears that our doubts were needless. Van Someren (1956, p. 221) writes that he has seen a "variegated honey-guide struggling into a hole scarcely large enough for her to enter."

2. Greater honey-guide, *Indicator indicator*

The new data on this, the best known of the honey-guides, whose recorded hosts now number 32 species, or, including subspecies, 38 forms, are as follows:

Striped kingfisher, *Halcyon chelicuti chelicuti* (Stanley)

Previously known from a single instance near Marandellas, Southern Rhodesia, this kingfisher is listed as a host by Smithers, Irwin, and Paterson (1957, p. 89), possibly on the basis of the same record. Neuby-Varty, the discoverer of the first case, has recently written me of what may be a second case. Early in December 1955, near Marandellas, he watched a striped kingfisher at a nest hole about 20 feet up in a tree. Suddenly, a freshly dead kingfisher nestling, about 4 or 5 days old, fell out of the opening and to the ground. He picked it up and noted tiny punctures anterior to the wings that looked very much like the bill hook wounds of a nestling honey-guide. Unfortunately, he was not able to get to the nest and so could not prove that there was a honey-guide chick present. It may be recalled that in the case of nestling ejection by the young honey-guide in a nest of the crested barbet (Friedmann, 1955, pp. 147–148) the young barbets were ejected alive and unharmed, possibly because the nest stump had been broken off and there was little depth left to the nest cavity, thereby making ejection easier. In the present instance, it may be that the depth was greater and the parasite did not attempt eviction until after it had immobilized its nest mate.

Cinnamon-breasted bee-eater, *Melittophagus lafresnayii oreobates* (Sharpe)

In his recent book, van Someren (1956, p. 190) writes that he has taken eggs of the greater honey-guide from nests of this species in Kenya Colony, but does not give any indication of how many such cases he found. In addition, W. R. Ingram informs me (in litt.) that he once found a nest of this bee-eater, also in Kenya Colony, containing one egg of *Indicator indicator* as well as some pecked eggs of the host. This bee-eater was not known to be parasitized prior to these observations.

Crested barbet, *Trachyphonus vaillantii vaillantii* Ranzani

To the two records given in my book (1955, pp. 147–148) may be added two more, both of parasitized nests found in Southern Rhodesia by C. T. Fisher, and mentioned to me by Mr. H. M. Miles (in litt.)

Banded sand martin, *Riparia cincta cincta* (Boddaert)

One record for this hitherto unrecorded host, but the identification of the species of honey-guide involved is only inferential. Captain R. H. Stevenson informs me that a honey-guide's egg was found in a nest of this swallow in the Selukwe Reserve, Southern Rhodesia, about the end of November or the first days of December 1955. It is possible that either *Indicator indicator* or *I. minor* might be involved. In the absence of details, such as notes on the status of the two in that locality, dimensions of the egg, etc., it is not possible to allocate the record. It would seem more likely to be *I. indicator* because that species makes use of nests in holes in the ground much more frequently than does *I. minor*, but both are known to do so. In their recent book on the birds of Southern Rhodesia, Smithers, Irwin, and Paterson (1957, p. 89) list this swallow as a host of the greater honey-guide. I do not know if this is based on Captain Stevenson's record or if it is still another case.

Kenya anteater-chat, *Myrmecocichla aethiops cryptoleuca* (Sharpe)

Previously only two records were known to me, to which two more may now be added, indicating more definitely something of the regularity, if not frequency, with which this species is parasitized. W. R. Ingram informs me that he has found two nests of this bird, each containing a single egg of the greater honey-guide in addition to several pecked eggs of the host.

Red-shouldered glossy starling, *Lamprocolius nitens* (Linnaeus)

To the single host record recorded in my book (1955, p. 152) may be added another, unfortunately without exact data. Mr. C. H. Jerome informs me that he has been told of a second such occurrence, but did not have any explicit information about it.

Blue-eared glossy starling, *Lamprocolius chalybeus chalybeus* (Hemprich and Ehrenberg)

The southern subspecies of this starling, *L. c. sycobius* Hartlaub, was previously known to be parasitized by the greater honey-guide in the northern Transvaal. We may now note the same for the nominate race. Mr. W. R. Ingram writes me that at Serere, Teso District, Uganda, on Mar. 22, 1956, he found a nest of this bird containing a single egg of the greater honey-guide, together with some pecked eggs of the starling.

3. Lesser honey-guide, *Indicator minor*

Recent data of interest involve three species of hosts, one of them previously unrecorded in this capacity.

Striped kingfisher, *Halcyon chelicuti chelicuti* (Stanley)

Previously (Friedmann, 1955, p. 193) I knew of two records, both in South Africa. To these may be added a third, somewhat indefinite one from Kenya Colony, where van Someren (1956 p. 221) found an egg attributed to the lesser honey-guide in a nest of this little kingfisher.

Cinnamon-breasted bee-eater, *Melittophagus lafresnayii oreobates* (Sharpe)

Van Someren (1956, p. 190) has found this bee-eater to be parasitized by the lesser as well as by the greater honey-guide in Kenya Colony. This is an addition to the known victims.

Pied barbet, *Tricholaema leucomelan* (Boddaert)

Previously known as a frequent victim in South Africa, this barbet is now recorded in this capacity in Southern Rhodesia as well, where, according to H. M. Miles (in litt.), Irwin found a nest containing a young lesser honey-guide as the sole occupant.

Although only of suggestive interest, mention may be made of the fact that in Ghana, between Accra and Kumasi, early in June, Donald W. Lamm (in litt.) watched a colony of brown barbets, *Gymnobucco calvus*, ready to begin breeding. At least four lesser honey-guides (*Indicator minor ussheri*) were present. They were very quiet, perching on the heavier branches of the trees, and showed no attempts to enter any of the nest holes. Two of them, a male and a female, were collected, both with well-developed gonads. This observation suggests that this species of barbet, as well as *Gymnobucco bonapartei* (already so recorded by Friedmann, 1955, p. 193), may be a host of the lesser honey-guide.

4. Slender-billed honey-guide, *Prodotiscus insignis*

To the little known information about the hosts of this honey-guide previously compiled by me (1955, pp. 251–252) may be added further details of the cases there described, as well as one additional host species. Like the previous data, the new observations all stem from Dr. van Someren.

Black-throated wattle-eye, *Platysteira peltata peltata* Sundevall.

Of this host all I was able to report previously (Friedmann, 1955, p. 251) was the bare fact that van Someren had once found a parasitized nest. He (van Someren, 1956, pp. 281–283) recently supplied more data, of which the following is a summary. When the nest was found, it contained just the young honey-guide, dark brown with a yellow gape, and quite naked. "The chick grew rapidly and on the fourth day of observation was well feathered on the head and back. It was then that I saw that . . . the plumage being gradually assumed was the olive green of a pigmy honey-guide. . . . The youngster was now receiving quite large moth larvae, imago moths, and dozens of small Diptera." Shortly afterwards some predator robbed the nest and ended the opportunity for further observation.

Kikuyu green white-eye, *Zosterops virens kikuyuensis* (Sharpe)

To the case I previously recorded (Friedmann, 1955, p. 252) merely as having two young slender-billed honey-guides in the nest, van Someren's (1956, pp. 222–223) additional data provide the following details. He found one of the young parasites just out of the nest on the ground near his house. As he was looking to see what nest it may have come from, he saw one of the white-eyes fly with food to a chick in a nest directly above the spot where he had picked up the fledgling. When his son climbed to the nest, the chick in it fluttered to the ground; it was found to be another slender-billed honey-guide. Van Someren put the two young birds in a cage, to which both parent white-eyes came with food for the next two days. The next night it rained very heavily and, as a result, one of the chicks died. The other one continued to be fed by the foster parents and was last seen in a tree nearby with the attendant white-eyes. Van Someren concludes his account by stating that the original white-eyes' eggs had been disposed of and that the honey-guide laid more than one egg in the white-eyes' nest. In view of the relative scarcity of these honey-guides, it does seem more probable that the two eggs in this nest were laid by one hen rather than by two, but this is only an inference. Similarly, we have no knowledge as to whether the host's eggs were removed by the laying honey-guide or ousted by the nestlings. In another place in his book, van Someren (1956, p. 434) does state that the hen honey-guide removes the victim's eggs one at a time when laying her own, but he gives no substantiating evidence for this statement.

Amethyst sunbird, *Chalcomitra amethystina kalckreuthi* (Cabanis)

This sunbird is an addition to the known victims of the slender-billed honey-guide. In November 1956, at Ngong, Kenya Colony, G. R. C. van Someren saw a newly fledged young slender-billed honey-guide being fed by both members of a pair of amethyst sunbirds. He watched them for some time at a distance of less than 10 feet.

Mammalian Symbionts

It is well established that the original foraging symbiont of the greater honey-guide is the ratel or honey-badger, *Mellivora capensis,* and that the human has deliberately become a substitute symbiont in its place. In my earlier account (1955, pp. 41–50) I gave some data to indicate that very occasionally baboons might be involved, and cited one instance of a bird apparently attempting in vain to evoke response from a mongoose, *Myonax cauui.* Verheyen (1951, pp. 91–93; 1957, pp. 105–113), on the other hand, suggested that the honey-guide may attempt to "call" to any or all of the larger mammals, between which he assumed it could not or did not distinguish. I find it difficult to agree with Verheyen in this matter and look upon the mongoose incident as an occasional error on the bird's part. However, the fact that as un-ratel-like a creature as the African human could become accepted as a symbiont shows that there may be a basic symbiont tolerance beyond what normally transpires. In this connection, it is of interest to record the following incident involving a greater honey-guide and a genet, kindly sent me by Bryan Neuby-Varty, who made the observation on his farm near Marandellas, Southern Rhodesia.

One day he was out in the brush when he heard a honey-guide calling and wondered if it was calling to any creature. Moving carefully he got behind a large tree and could see that it was watching a genet (probably *Genetta genetta mossambica*) on the ground at a hole at the base of a tree from which swarms of bees were flying. As long as the bird kept calling, the genet remained motionless, but soon it disappeared up to its shoulders down the hole, apparently not minding the bees. In a short while, it backed out with a small piece of beescomb which it proceeded to eat. Neuby-Varty then moved to a better position on a termite mound about 30 yards from the genet, from which spot he watched it for about half an hour as it repeatedly inserted its paw into the hole, pulled out pieces of comb, and proceeded to eat them. Then the wind changed and the genet must have scented the observer and it slunk off into the tall grass and was gone. Examination of the hole convinced Neuby-Varty that it was not dug by the genet but may have been the work of a jackal or possibly a mongoose or a ratel, although he has never seen the last named animal on his land.

In the above incident, there is no evidence that the bird had guided the genet to the hive, which apparently had been opened previously. It is more likely that the bird was attracted to the spot because of the bees, and its interest was then transferred to the genet that had come there independently and which, by virtue of its feeding there, actually kept the bird from doing the same. After the genet had left, the bird called intermittently for about 10 minutes and Neuby-Varty waited another 20 minutes to see if the beast would return. In those 30 minutes, the bird hopped down to the ground only once and pecked at tiny bits of comb.

We still have too few observations of associations between the greater honey-guide and various mammals, but it does seem that observations such as this one, or the one involving the mongoose, and even the baboon incident recorded earlier (Friedmann, 1955, pp. 45–46), hardly justify looking upon these creatures as definitely proved symbionts of the bird in the sense that ratels and humans are.

The Termination of Guiding Behavior

In my detailed account (Friedmann, 1955, pp. 25–71) I stated that the stimulus which appears to bring to a halt the guiding behavior, released earlier by the bird meeting with a potential foraging symbiont such as a ratel or a human, "is the sight or sound of bees. It is tempting to expand van Uexküll's and Lorenz's fruitful concept of the 'kumpan,' or companion, as the releaser of instinctive actions in birds and apply it to the honey-guides . . . . From this standpoint guiding may be looked upon as the result of the reactions evoked in the bird when the releasing agent is met with in the bird's natural environment, away from the bees' nest, for which it is the 'kumpan,' and the 'guiding' behavior is 'satisfied' or, at least, brought to a stop when the bird brings together the 'bee companion' and the bees." While I still think this statement is as close to the actual picture as present understanding permits, it has seemed to me possibly a little forced in its reasoning. It was, therefore, with considerable interest that I recently came across, in Russell's (1953) description of the drive character of instinctive behavior, some ideas that give further support to the applicability of the "kumpan" concept to guiding activities.

In the current general theory of instinct, we find that usually a chain of actions grouped under one heading as instinctive behavior tends to be divided into two phases, an introductory one of openly seeking, striving, appetitive behavior, and a directly subsequent one of essentially consummatory action, generally of a quasi-mechanical or quite stereotyped nature. The emphasis on the innate drive character of instinctive behavior, developed largely by Lorenz and his colleagues, seems warranted.

These investigators account for the specificity of the drives by hypothesizing what they term "action specific energy," which is said to accumulate and to be discharged with and into highly specific appetitive behavior patterns. Lorenz (1950) further assumes "that some sort of energy, specific to one definite activity, is stored up while this activity remains quiescent and is consumed in its discharge." Russell sees no real need to hypothesize energy when all that seems to be "accumulated" may be described just as readily as "specific tension or unreleased tendency to carry out a certain course of action." Regardless of whether it is a specific energy or a specific tension, the fact remains that we have, in either case, a support for what I implied when I wrote that the guiding behavior was "satisfied" and brought to a halt when both the bees and the bee "kumpan" simultaneously came to be within the sensory range of the bird. The specific energy is discharged, or the specific tension is dispelled, when the guiding bird achieves the unison of the releasing agent, the foraging symbiont, and the thing with which the releaser is associated in the experience of the activated bird, the bees. The mode of termination of guiding is one more example of the increasingly obvious fact that it is the discharge of consummatory action and not the biological or survival value involved that is the goal of innate appetitive behavior as far as the individual bird is concerned.

The Rustling Flight

The rustling flight, recorded for both the greater and the lesser honey-guides (Friedmann, 1955, pp. 130–133, 184), is of interest not only for itself but as the possible root from which evolved the highly specialized performance of the lyre-tailed honey-guide, *Melichneutes robustus*. The evidence is somewhat divided as to whether the rustling sound is produced by the wings or the tail in the greater and lesser honey-guide species, while in the lyre-tail it seems obvious that the sound is made by the highly peculiar outer tail feathers.

Two interesting additional observations have come to me, both having to do with the greater honey-guide. Neuby-Varty writes me that about the end of May, on his farm near Marandellas, Southern Rhodesia, he heard a greater honey-guide giving its *victor* call from the top of dead branches of a tree. Then it flew towards him, and just as the bird came above him, it started to make a rattling noise, apparently with its wings. The tail may have been involved as well, as the bird spread it fanwise while making the noise. Neuby-Varty timed the performance and found the noise (written down as *feet-up*) was given 10 times, with an interval of about a second between the sounds.

W. R. Ingram, at Serere, Uganda, informs me that he has found the rustling or drumming flight to be given only towards evening and always in the early dry season. He thinks it has no connection with courtship, as there are no suitable hosts nesting at the time of the year. He first heard it in December 1955, at about 7 p. m. and almost dark; the noise "was most eerie and seemed to come from different parts of the sky almost at once, showing that whoever or whatever was making the noise was moving very fast indeed." Ingram describes the sound made by suggesting that if one blows out the word *whukooo* with a great expulsion of air on the first syllable and with strong emphasis on the *K*, and then emptying one's lungs on the *ooo*, a similar sound can be produced. He goes on to say that "the noise was heard occasionally at dusk during the whole dry season (December–March) and again in 1956, but the author was never discovered." It was not until 1957 that he succeeded in seeing as well as hearing the performing bird. Early in December of that year, at about 6 p. m., he saw the bird

> . . . traveling at a very high speed in a circling, dipping flight. It careened around the sky for about 30 seconds and then dived into a large tree . . . . Immediately, three or four *victor* notes came from this very tree . . . . I knew this tree to be a popular stud-post, all the year round, but still I could not connect the bird in the sky with the honey-guide.
>
> However, I did not have to wait very many evenings before I got a repeat performance. I managed to pick up the bird in flight with the binoculars during its drumming flight, follow it round and into the same stud-post. At the moment it darted into the tree, if fanned its tail and the outer white feathers were very conspicuous; this is the only time it opened its tail in flight, so I assume the noise is done with the wings. It landed on a prominent perch and I got close enough for a positive determination . . . .

This account indicates a similarity in habit to the aerial evolutions of the lyre-tail even more definitely than did our previous data. It also supports the observations of Ranger, Neuby-Varty, and myself that the sound is produced by the wings and not by the tail.

Feeding Habits

That fair numbers of honey-guides may occasionally gather to eat at a single bees' nest is shown by an observation sent me by H. F. Stoneham, who heard noises coming from one of his domestic beehives. Thinking that a rat or some other creature was raiding the nest, he went to it, and was surprised to see eight honey-guides fly out in rapid succession, six greaters and two lessers.

Kettlewell (1955, pp. 45–47) describes a nest of wild bees built in an abandoned wrecked automobile, the metal of which became hot from the sun and caused the honey inside to ferment. This apparently had intoxicated a greater honey-guide, which Kettlewell pulled out of the automobile.

An addition to the known diet of the lesser honey-guide is reported by van Someren (1956, p. 221), who saw one taking the young larvae and pupae from the paper nest of an aculeate wasp. This recalls the old observation of Butler, Feilden, and Reid (1882, p. 208) who reported the greater honey-guide pecking at the comb of a wasp's nest that had fallen to the ground.

Chapin has recently sent me some observations on the feeding habits of the least honey-guide, *Indicator exilis*, in the eastern Belgian Congo. He opened an old bees' nest in which he found considerable quantities of comb, practically empty of honey. The next day a least honey-guide came to it, and again two days later he saw one there. He placed a piece of the comb in a branch of a tall bush where he could watch it, and the bird came there and ate pieces of the comb. The bird was alone in each case, which fact seems to answer Chapin's (1939, p. 540) earlier statement that since this species does not guide humans, it may have some other mammalian symbiont.

Chapin observed not only the least honey-guide feeding at open bees' nests, but also his newly discovered pigmy honey-guide, *Indicator pumilio*. In fact, most of his specimens of the latter were captured with a butterfly net as they emerged from a beehive.

Recently Verheyen (1957) has taken objection to my conclusion that the primary interest of the honey-guides in bees' nests is the wax of the comb rather than the honey, pollen, or bee larvae. It should be pointed out that I have described that the birds do eat the bee larvae and pupae, and, adventitiously, the honey, but it still remains that the wax is the one substance they are most eager to get from the hive, and the one substance they cannot obtain elsewhere. They are constantly catching insects on the wing, and are certainly not primarily wax feeders. As I pointed out, honey-guides grow to full size in their hosts' nests without getting any wax in their food, but once they begin feeding for themselves they eat wax avidly, not as a substitute for some other food but as an addition to their diet. By itself, beeswax is not a "total" food as it lacks nitrogen, without which no bird could survive for more than a few weeks or a month.

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